Why do wild bonobos not use tools like chimpanzees do?

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Why do wild bonobos not use tools like chimpanzees do?

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Running head: Tool use among *Pan* species

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Abstract

One of the most conspicuous behavioural differences among great apes is the paucity of tool use among wild bonobos (*Pan paniscus*) in comparison to chimpanzees (*Pan troglodytes*) who are one of the most prolific and skilled tool users in the animal kingdom. This is in spite of the fact that bonobo tool use repertories are as large and diverse as chimpanzees in captive settings. In this study, we compared tool using behaviours and potential drivers of these behaviours in the Wamba bonobo population located in central Democratic Republic of Congo with the Goualougo chimpanzee population of northern Republic of Congo. The tool use repertoire of wild bonobos was comprised of only 13 behaviours, compared to 42 for chimpanzees. However, the number of tool behaviours observed in each study site was similar between bonobos and chimpanzees, and many types of tool use for social purposes and for self-comfort or protection were commonly used by both species. A marked difference is that 25 of 42 tool behaviours exhibited by chimpanzees are performed for feeding, in contrast to a single report of bonobos using a leaf sponge to drink water. We examined whether the differences in tool use repertoires can be explained by the necessity, opportunity, relative profitability, or invention hypotheses. We found that habitat composition, seasonal fluctuation of temperature and rainfall, and fluctuation of fruit production at these two sites were similar, particularly when compared with variation observed between sites within each species. Thus it was

unlikely that the necessity hypothesis explains the lack of tool use for feeding in bonobos. Though further study at Wamba is needed, we did not identify any obvious differences in prey availability that would indicate differences in tool using opportunities between the sites. This study could not test the relative profitability hypothesis, and further research is needed on whether tool use is the most efficient means of calorie or protein intake for wild apes. Bonobos at Wamba formed much larger and stable parties than chimpanzees at Goualougo, which was contrary to the prediction by the invention hypothesis. Another explanation is that differences in tool use behaviour between bonobos and chimpanzees might not be explained by the current ecological or social conditions, but rather by circumstances during the Pleistocene Epoch. The observed species differences might also reflect divergent behavioural predispositions, rather than actual differences in cognitive abilities.

Introduction

Comparisons of bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*) lifestyles have revealed several intriguing differences between these closely related apes (Fruth, Hohmann et al. 1999). These allopatric species reside in the equatorial forests of Africa, separated by the Congo River. They both live in multi-male multi-female groups with male philopatry and a fission-fusion social structure (Kano 1982). One of the most conspicuous behavioural differences between these apes is the rarity of tool use among wild bonobos in comparison to chimpanzees who are one of the most prolific and skilled tool users in the animal kingdom (McGrew 1992, Sanz and Morgan 2007, Shumaker, Walkup et al. 2011). An increased knowledge of the ecology and sociality of wild bonobos and the central subspecies of chimpanzee (*P. t. troglodytes*) now makes it possible to examine the specific environmental and social factors which may elicit tool use among chimpanzees and bonobos. Such a comparison is particularly informative because chimpanzees inhabiting the Congo Basin exist within habitat types that are more similar to bonobos than other chimpanzee subspecies residing at the edges of the species range. In this study, we compare tool use behaviours and potential drivers of these behaviours in the Wamba bonobo population located in central Democratic Republic of Congo with the Goualougo chimpanzee population of northern Republic of Congo.

Despite years of field research at multiple study sites, there are few reports of

71 tool use by bonobos in natural settings (Kano 1982, Ingmanson 1996, Hohmann and
72 Fruth 2003). As we will show in this paper, the species repertoire is comprised of 13 tool
73 use behaviours, compared to more than forty for chimpanzees (Sanz and Morgan 2007).
74 In striking contrast to chimpanzees, there are no reports of bonobos using tools in a
75 feeding context except using a leaf sponge to drink water. This is despite the fact that
76 bonobos are capable of using tools to obtain food, as shown by reports from captive
77 populations (Jordan 1982, Gold 2002, Gruber, Clay et al. 2010, Shumaker, Walkup et al.
78 2011, Boose, White et al. 2013).

79 Ecological and social factors are typically examined in isolation, but it is likely
80 that a combination of these factors shape the emergence and maintenance of tool use in
81 natural settings. Recent studies addressing the drivers of tool use cite some iteration of
82 the Necessity and Opportunity Hypotheses, which state that tool use is a behavioural
83 response to the absolute abundance of ecological resources or opportunities in the
84 environment (Spagnoletti et al. 2012; Koops et al. 2013; Sanz et al. 2013). More
85 specifically, the Necessity Hypothesis posits that tool use is a response to resource
86 scarcity which drives its practitioners to exploit novel food items during times of low
87 resource availability (Fox, Sitompul et al. 1999). The Opportunity Hypothesis proposes
88 that repeated exposure to appropriate conditions, such as encounters with target items
89 and availability of tool materials, prompts the emergence and/or maintenance of tool use

behaviours (Fox, Sitompul et al. 1999). Shifting the emphasis away from absolute abundance, the Relative Profitability Hypothesis suggests that tool-assisted feeding strategies targeted at embedded food items would be expected when it is more profitable than conventional methods of gathering more accessible foods (Rutz, Bluff et al. 2010, Rutz and St Clair 2012). Representing the social forces in the evolution of tool use, the Invention Hypothesis states that "behaviours such as tool use are rarely invented, and that the spread and maintenance of such behaviours requires sufficient opportunities for observational learning via social proximity to conspecifics (p.163)" (Fox, van Schaik et al. 2004). Recent research in both wild and captive settings has led to increasing recognition of the role of social transmission in maintaining technological traditions (Lonsdorf 2006, Whiten, Spiteri et al. 2007).

The aim of this study is to review differences in bonobo and chimpanzee tool use repertoires and assess to what extent these differences can be attributed to necessity, opportunity, relative profitability, or invention (Table 1). We address these hypotheses using behavioural observations and ecological data from bonobos at Wamba in Democratic Republic of Congo and chimpanzees of the Goualougo Triangle in Republic of Congo. 1) The absence of tool use for feeding by bonobos would be explained by the Necessity Hypothesis if their preferred foods are more abundant and if they experience a lesser degree of seasonal resource scarcity than chimpanzees. 2) To explain the absence of

feeding tool use by bonobos, one might also postulate that tool use opportunities are absent or far less abundant in bonobo habitats than chimpanzee habitats, which would support the Opportunity Hypothesis. 3) The Relative Profitability Hypothesis predicts that the energetic gains of tool-assisted strategies exceed that of conventional feeding. 4) With regard to the Invention Hypothesis, one could predict that chimpanzee parties are larger and thus provide more opportunities for social transmission of technological information among adult individuals. In this manuscript, we also summarize and propose additional possible explanations and evolutionary scenarios for the differences in tool use between *Pan* species.

Methods

Wamba, Democratic Republic of the Congo.

The Wamba study area is located in the northern section of the Luo Scientific Reserve (E 22°34'; N 0°01'), Democratic Republic of the Congo. This area is included in the Congo-equatorial climatic zone. The main habitat type is primary forest, including some areas of old secondary forest. This habitat type occurs on terra firma and is characterized by species of the Caesalpiniaceae family, with some narrow bands of monodominant *Gilbertiodendron dewevrei* forest occurring along the boundaries of

swamp forests. The second main habitat type is swamp forest that exists along the Luo River and its tributaries. Most of the swamp forest is inundated all year, but a part of it near the terra firma is seasonally inundated. This habitat type is characterized by a complex mosaic of species, mainly representing the Caesalpiniaceae and Euphorbiaceae families. The northern section of the Luo Scientific Reserve contains homesteads, and so this area also includes agricultural complexes and young secondary forest (Idani, Kuroda et al. 1994, Hashimoto, Tashiro et al. 1998).

Rainfall and temperature were recorded daily in the research camp located in a homestead at Wamba, using a stationary rain gauge and thermometers with minimum and maximum temperature.

To monitor fruit abundance, we used five line transects and reconnaissance paths, the total length of which was 22,550 m (Mulavwa, Furuichi et al. 2008). Each trail was surveyed twice a month. We recorded the number of clusters of fallen fruit that were found within 1 m on each side of the trail, the number of fruits in each cluster, species of fruit, and whether they were ripe or unripe. The validity of this approach was established by Furuichi et al. (Furuichi, Hashimoto et al. 2001) who showed that the abundance of chimpanzee fruit foods at Kalinzu in Uganda was sufficiently evaluated by the number of clusters of ripe fallen fruits. Furthermore, Mulavwa et al. (Mulavwa, Furuichi et al. 2008) compared the numbers of ripe-fruit clusters of all species and the food species of bonobos

147 at Wamba, and found that these numbers fluctuated proportionately. Therefore, in this
148 study, we evaluated abundance of fruit foods based on the number of clusters of ripe
149 fallen fruits of all species per km of transect.

150 A main study group of bonobos, group E, was habituated to the presence of
151 researchers and has been observed since 1976. The group has subsequently split into two
152 groups, E1 and E2. Another group, P, was also habituated and has been observed since
153 the 1980's. Observations were made using artificial provisioning during some part of each
154 year until 1996, but currently groups E1 and P are being observed from nest to nest
155 under the natural conditions (Kano 1992, Furuichi, Idani et al. 2012). In November 2012,
156 group E1 consisted of 31 individuals, including 7 adult males and 9 adult females, and an
157 eastern subgroup of P that is also continuously monitored by researchers consisted of 26
158 individuals, including 5 adult males and 7 adult females.

159 Tool use behaviours have been documented through direct observation
160 throughout the study period (Kano 1982, Ingmanson 1996). In this study, we report
161 previously unpublished observations of tool use behaviours by bonobos at Wamba that
162 were made before the end of 2012.

163 We employed the definition of the 1-hour party size proposed by Hashimoto et al.
164 (Hashimoto, Furuichi et al. 2001) for evaluating party sizes of chimpanzees. While
165 following a party, we recorded the names of all bonobos in sight at the beginning of each

hour and continued recording those bonobos that appeared in the party throughout the rest of the hour. Thus, the 1-hour party represents the minimum number of bonobos that were present in the party during each 1-hour observation. We also recorded the observation time in minutes in each 1-hour segment. We obtained the daily 1-hour party size by averaging all those observations recorded in a day, excluding those with less than 30 min of observation.

Goualougo Triangle, Republic of Congo.

The Goualougo Triangle study area is located along the southern boundary of the Nouabalé-Ndoki National Park (E 16°51'-16°56'; N 2°05'-3°03'), Republic of Congo. The climate in northern Republic of Congo can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones. The lowland tropical forests of northern Congo are part of the regional centre of endemism Guinea–Congolian that ranges from Nigeria to the Congo Basin (White 1986). The different habitat types in the Goualougo Triangle have been assessed by ground surveys and satellite imagery classification (Devos, Sanz et al. 2008). The main habitat types are mixed-species forest (semi-deciduous forest with high heterogeneity of species composition and occurs on terra firma), monodominant *Gilbertiodendron dewevrei* forest (single-species formation of *G. dewevrei* which occurs along watercourses as well as on interfluvial plateaus), and

185 gallery/swamp forest (consists of diverse flora associated with watercourses, that may be
186 permanently or seasonally inundated).

187 Rainfall and temperature were recorded daily in the Nouabalé-Ndoki National
188 Park. Stationary rain gauges and thermometers with minimum and maximum
189 temperature gauges were stationed in the Goualougo Triangle.

190 Relative abundance of preferred chimpanzee foods was systematically assessed
191 through establishment of two trail networks to monitor the phenological states of tree
192 species and strangler figs known to be consumed by apes (Chapman, Wrangham et al.
193 1994). A total of 607 trees representing 47 species were monitored each month in the
194 Goualougo Triangle. The ground under each monitored tree was systematically surveyed
195 to determine the abundance of mature fruit fall. Relative abundance of fruit was
196 estimated on a scale of 0 to 4, with higher scores indicating more fruit. In this study, we
197 evaluated abundance of fruit foods based on the proportion of monitored trees with
198 mature fruit fall.

199 Direct observations of the chimpanzees in the Goualougo Triangle have been
200 ongoing since February 1999. Individual chimpanzees were identified from their distinct
201 physical characteristics and these data compiled in a population history database. The
202 main study group is the Moto community which consisted of 71 individuals, including 17
203 adult males and 24 adult females (Morgan 2007).

Tool use behaviours have been documented through direct observation during reconnaissance surveys of chimpanzees since the initiation of research at this site. In 2003, we also began remote video monitoring of tool use sites. For all observations of tool use, observers record the identification of the chimpanzee, type of object used, target of object, actions, context and/or goal of the tool use behaviour, and the outcome.

20-minute group scans of party composition and behaviour were recorded during chimpanzee encounters. Chimpanzee parties were considered to be all individuals travelling, feeding, resting or socializing within 50 m of one another (definition adopted from (Wrangham, Clark et al. 1992, Wilson, Hauser et al. 2001)). For this study, we included information from the first scan conducted each hour so as to provide a direct comparison with the 1-hour sampling of bonobo party size at Wamba. Daily values of party size were based on average sizes of all recorded 20-min group scans per day, excluding those with only orphans present.

Results

Habitat Types and Climate

Bonobos and chimpanzees inhabit a wide range of habitats across equatorial

223 Africa (Table 2). The habitat types of bonobos range from savannah with patches of forest
224 with 1,666-1,778mm annual rainfall at Lukuru to rain forest with 2,733mm rainfall at
225 Wamba, while that of chimpanzees range from grassland and woodland with 954mm
226 rainfall at Assirik to rain forest with 3,244mm rainfall at Seringbara. Thus, the habitat
227 conditions of bonobos and chimpanzees largely overlap with an exception of the driest
228 extreme in chimpanzees.

229 Habitat classification of satellite imagery showed that the Wamba forest is
230 comprised mainly of primary and old secondary forest dominated by representatives of
231 the Caesalpiniaceae family (65.5%), with swamp forest (18.9%) and young secondary
232 forest (15.6%) representing a smaller proportion of the bonobo range (Saeko Terada et al.,
233 unpublished data) (Hashimoto, Tashiro et al. 1998). Mixed species semi-evergreen forest
234 (71.5%) was found to be the dominant habitat in the Goualougo Triangle, with
235 monodominant *Gilbertiodendron dewevrei* (Caesalpiniaceae) evergreen (21.7%) and
236 swamp forest (6.1%) also represented (Devos, Sanz et al. 2008).

237 Our site-comparison revealed that temperature and its pattern of fluctuation was
238 similar between Wamba and Goualougo (Figure 1a). If we compare 37 months for which
239 data are available for both sites, the monthly mean of the daily maximum temperature is
240 slightly higher for Wamba (Wamba: 25.4±0.6(S.D.), Goualougo: 23.7±0.8, matched-pair
241 t-test, $t=12.3$, $df=36$, $p<0.0001$) and the monthly mean of the daily minimum temperature

was slightly lower for Wamba (Wamba: 20.8±0.3, Goualougo: 21.4±0.3, t=5.7, df=36, $p<0.0001$), but the mean temperatures were similar. Both sites showed seasonal changes in maximum and minimum temperature, but the seasonal shifts were similarly small (C.V. for maximum temperature: Wamba: 0.036, Goualougo: 0.032; C.V. for minimum temperature: Wamba: 0.027, Goualougo: 0.023).

The annual rainfall was greater at Wamba (Wamba: n=7 (2004-2006, 2008, 2010-2012), 2733±283 (S.D.) mm) than at Goualougo (Goualougo: n=5 (2007-2011), 1690±27 mm) (Figure 1b). There was a significant difference when we compared the years 2008, 2010, and 2011 for which data were available for both sites (matched-pair t-test, $t=-4.96$, df=2, $p<0.05$). Seasonal patterns of rainfall were similar between these sites, with rainfall showing monthly fluctuations and a dry season occurring at the beginning of the year (Wamba: 232.8±106.8 mm, C.V.=0.46, N=109; Goualougo: 141.3±87.6 mm, C.V.=0.62, N=67). Thus differences in temperature and rainfall exist between Wamba and Goualougo, but they seem to be fairly small as compared to variations found in each species (Table 2).

Ape Density, Home Range and Habitat Use

Ape densities were nearly identical between the two study sites. At Wamba, bonobo densities were reported to be 1.4 to 2.5 individuals/km^2 (excluding infants) based

261 on home range estimates (Hashimoto, Tashiro et al. 1998). Chimpanzee density in the
262 Goualougo Triangle was estimated to be 1.5 chimpanzees/km^2 (excluding infants) from
263 line transect surveys and 2.2 chimpanzees based on home range estimates (Morgan, Sanz
264 et al. 2006). The home ranges of bonobo communities at Wamba were estimated to be 12.3
265 to 17.8 km^2 for the E1 study group and 22.5 to 31.5 km^2 for the E2 study group
266 (Hashimoto, Tashiro et al. 1998). The Moto chimpanzee community range was estimated
267 to be 17.3 to 19.2 km^2 (Morgan, Sanz et al. 2006). The home ranges of both species were
268 heterogeneous in habitat composition, but with some evidence of preference for dry forest
269 habitats by both bonobos and chimpanzees. Both direct observations of habituated groups
270 and nest surveys indicated that use of swamps by bonobos may exceed visitation to
271 inundated habitats by chimpanzees (Hashimoto, Tashiro et al. 1998, Morgan, Sanz et al.
272 2006, Mulavwa, Yangozene et al. 2010).
273
274 **Tool Use Repertoire**
275 The bonobo tool use repertoire was comprised of 13 different types of tools (Table
276 3), with eight types of tool use exhibited by the Wamba population. Chimpanzees in the
277 Goualougo Triangle exhibited 22 different types of tool use, which is approximately half of
278 the species repertoire (Sanz and Morgan 2007). The number of tool behaviours found at
279 chimpanzee study sites varied from 22 in Goualougo to 6 in Assirik. Hence, the numbers

of tool behaviours at bonobos study sites (10 in Wamba and 8 in Lomako) are within the range of variation in chimpanzees (Table 4). Chimpanzee tool use was most common in feeding contexts, but was also exhibited in self grooming/stimulation, comfort/protection, and social situations. Bonobo tool use mainly had social and self-directed (self grooming/stimulation, comfort/protection) functions, except for one behaviour (leaf sponge) to drink water. Among 13 tool behaviours, 8 were common in chimpanzees and 5 were uniquely found in bonobos. Out of 4 chimpanzee universal tool behaviours, 3 were observed in bonobos (play start, drag branch, leaf-sponge) but 1 was not observed (investigatory probe).

A marked difference in tool behaviours between chimpanzees and bonobos is the very limited tool use for feeding in bonobos (Table 4). In chimpanzees, 25 of 42 tool behaviours were performed for feeding (Sanz & Morgan, 2007). By contrast, tool use for feeding was observed only once in Lomako, in the use of a leaf-sponge (Hohmann & Fruth, 2003). Therefore, what we really need to examine is why wild bonobos do not use tools for feeding.

Abundance of Preferred Resources

Similar to other bonobo and chimpanzee populations, the diet of apes at Wamba and Goualougo was primarily comprised of ripe fruits (Kano and Mulavwa 1984, Morgan

299 and Sanz 2006). As an indication of the overall abundance of food resources, we compared
300 the total basal area of all trees with DBH greater than 5 cm in Wamba and of all trees
301 with DBH greater than 10 cm in Goualougo. The basal area for Wamba is 33.27 sq meters
302 per hectare for primary forest (including secondary forest), 28.50 for swamp forest, 21.90
303 for young secondary forest (calculated from DBH^2 in (Idani, Kuroda et al. 1994)) and that
304 for Goualougo is 34.04 sq meters per hectare. (Morgan and Sanz 2006). Due to the
305 difference in sampling (inclusion of a larger sample of trees than Goualougo), the
306 per-hectare total basal area of trees at Wamba must be somewhat overestimated as
307 compared to Goualougo. Therefore, we can conservatively conclude that the total basal
308 area in Wamba is not greater than at Goualougo.

309 Though we do not have comparable data for absolute abundance of ripe fruit, we
310 compared the pattern of seasonal fluctuation in abundance using parameters that
311 represent proportion of trees with ripe fruit (Figure 1c). The monthly proportion of trees
312 with ripe fruit on the ground showed similarly stochastic fluctuations between the sites,
313 though the degree of fluctuation was greater in Goualougo (Wamba: 5.5±2.0 clusters per
314 km of transect, C.V.=0.35, N=61; Goualougo: 5.6±3.2% of monitored trees, C.V.=0.56,
315 N=67). When fruits were scarce, bonobos at Wamba increased their intake of seeds, leaves,
316 and terrestrial herbs (Kano and Mulavwa 1984), and chimpanzees in the Goualougo
317 Triangle similarly compensated by increasing their intake of leaves (Morgan and Sanz

318 2006, Sanz and Morgan In press).

319 Overall, although the degree of fluctuation in availability of ripe fruit was
320 greater in Goualougo, similar per-hectare tree basal areas and similar tendencies of food
321 shift during fruit scarcity, together with similar density of bonobos and chimpanzees
322 mentioned in the previous section, suggests that the differences in the food conditions
323 between Wamba and Goualougo were much smaller than differences among sites of each
324 species (Table 2).

325

326 **Ecological Opportunities for Feeding with Tools**

327 In the Goualougo Triangle, tools are used to harvest several species of termites
328 (*Macrotermes muelleri*, *M. lilljeborgi*), army ants (*Dorylus mayri, D. rubellus, D.*
329 *sjoestedti, D. wilverthi*), and the honey of stingless bees (*Trigona* spp.). Although we have
330 not yet assessed the availability and distribution of these different insect species at
331 Wamba, we confirmed that these insects (or their products) are present. Seemingly, there
332 are ample ecological opportunities (i.e. termites, army ants, bees, and suitable raw
333 materials) at Wamba for termite fishing, ant dipping, ant fishing, and honey gathering
334 tool use, which is similar to research findings at Lui Kotale (McGrew, Marchant et al.
335 2007). We also confirmed the presence of oil palms (*Elaeis guineensis*) at Wamba which
336 are the target of pestle pounding and nut cracking by chimpanzees at Bossou and other

337 sites (Humle and Matsuzawa 2004).

338

339 **Opportunities for Social Transmission of Technical Information**

340 As shown in Figure 1d, bonobos at Wamba consistently gathered in larger parties
341 than chimpanzees in Goualougo (monthly mean party size at Wamba: 9.4±2.2 animals,
342 CV=0.23, N=50; Goualougo: 3.5±1.3 animals, C.V.=0.36, N=97). There was a significant
343 difference in party size if we compared those in the periods for which data was available
344 for both sites (matched-pair t-test, $t=-15.1$, $df=38$, $p<0.0001$). This difference in party size
345 was further corroborated by mean nest group size of 9.3±4.9 (n=215, range: 1, 24) bonobo
346 nests in Wamba (Mulavwa, Yangozene et al. 2010) versus 2.75±1.88 (n=375, range: 1, 12)
347 chimpanzee nests in Goualougo (Morgan, Sanz et al. 2006, Mulavwa, Yangozene et al.
348 2010).

349 *Correlations among examined factors*

350 We also examined potential relationships among factors that may influence tool
351 use behaviours: rainfall, fruit abundance, and party size in each site. For Wamba, there
352 was no significant correlation in each pair of the factors (rainfall-fruit abundance: $r=0.08$,
353 $df=1, 56$, n.s.; rainfall-party size: $r^2=0.03$, $df=1, 46$, n.s.; fruit abundance-party size: $r=0.31$,
354 $df=1, 30$, n.s.). On the other hand for Goualougo, significant correlations were found
355 between rainfall and fruit, and between fruit and party size (rainfall-fruit abundance:

356 r=0.29, df=1, 65, p<0.05; rainfall-party size: r=0.01, df=1, 46, n.s.; fruit abundance-party
357 size: r=0.42, df=1, 46, p<0.01).
358
359 **Discussion**
360 The aim of this study was to review differences in chimpanzee and bonobo tool
361 use and examine whether these differences could be attributed to current hypotheses
362 outlining various ecological and social factors suggested to be responsible for the
363 emergence and maintenance of tool traditions (Table 1). Our comparison of tool
364 behaviours between bonobos and chimpanzees revealed that the main difference between
365 the two species exists in their repertoires of tool use for feeding, which is large and
366 diverse in chimpanzees and nearly absent in bonobos. Furthermore, our comparisons of
367 ecological and social conditions between Wamba and Goualougo, and comparisons of
368 habitat conditions across various *Pan* study sites, suggested that it is difficult to explain
369 the differences in tool use repertoires between the two species based on current ecological
370 or social conditions. Our review of current evidence for *Pan* tool use led us to conclude
371 that understanding the differences in the expression of tool use between chimpanzees and
372 bonobos will require alternative ecological, behavioural, or social explanations.
373 In the reported difference in tool use between wild bonobos and chimpanzees, we
374 may have another overemphasized contrast or false dichotomy between the two *Pan*

375 species (Stanford 1998, Fruth, Hohmann et al. 1999). The size of the Wamba tool
376 repertoire was smaller than that of chimpanzees but still within the range of the number
377 of tools used by some chimpanzee populations in East Africa (Sanz and Morgan 2007).
378 Although we did not quantify the frequency of tool use in this comparison, our impression
379 is that tool use was less frequently exhibited by bonobos than chimpanzees. This species
380 difference is largely due to the fact that wild bonobos do not use tools in feeding, except
381 for a few observations of tool use for drinking water by bonobos in Lomako (Hohmann and
382 Fruth 2003). In the Goualougo Triangle and in other chimpanzee populations,
383 tool-assisted feeding occurs on a regular basis and can occupy a significant portion of the
384 daily activity budget (Pandolfi, van Schaik et al. 2003, Bogart and Pruetz 2011). Another
385 difference is the absence of investigatory probing in bonobos which is a universal
386 behaviour among chimpanzee populations (Whiten, Goodall et al. 2001). Many of the
387 behavioural elements involved in investigatory probing can be generalized to
388 tool-assisted feeding situations that involve probes or dipping implements, such as
389 termite fishing, ant dipping, or fluid dipping (Sanz and Morgan 2010). It has been
390 well-documented that bonobos have the physical and cognitive abilities to exhibit such
391 tool behaviours (Gruber, Clay et al. 2010, Boose, White et al. 2013), and so there may
392 exist ecological or social factors which elicit these tool use behaviours in wild
393 chimpanzees, but not in bonobos.

394 For the Necessity Hypothesis to explain the difference in bonobo and chimpanzee
395 tool use, we would expect to find that bonobos have a more stable food resource base than
396 chimpanzees. This would effectively alleviate the need for tool-assisted fallback strategies.
397 In support of this, chimpanzee tool use was negatively correlated with abundance of ripe
398 fruit at Bossou in Guinea (Yamakoshi 1998). In environments with few typically preferred
399 foods, tool use may also be a strategy to harvest staple food items. This may be the case
400 for some types of chimpanzee tool use at savannah sites, such as the termite gathering of
401 chimpanzees at Fongoli in Senegal (Bogart and Pruetz 2011) and possibly the tuber
402 harvesting by chimpanzees at Ugalla in Tanzania (Hernandez-Aguilar, Moore et al.
403 2007).

404 However, a recent review of studies that have explored the ecological dimension
405 of the presence or absence of technology clearly shows that necessity may play a less
406 prominent role in prompting and promoting tool use than previously suggested (Sanz and
407 Morgan In press). The Necessity Hypothesis was explicitly tested and a lack of support
408 was cited for nut cracking tool use by capuchins at Boa Vista in Brazil (Spagnoletti,
409 Visalberghi et al. 2012), tool use to extract insects from tree holes and extract seeds from
410 *Neesia* fruit by orangutans across Borneo and Sumatra (Fox, van Schaik et al. 2004), and
411 various forms of chimpanzee tool use at Seringbara in Guinea (Koops, McGrew et al.
412 2013). The Goualougo chimpanzee population also does not seem to compensate for the

413 lack of fruit resources by increasing their frequency of tool use for social insects or honey
414 (Sanz and Morgan In press). Rather, opportunities to gather termites, ants, and honey
415 were available throughout the year to this chimpanzee population and enhanced by the
416 use of tool sets (Sanz, Morgan et al. 2004, Sanz and Morgan 2009, Sanz, Schoning et al.
417 2010). Profiles of tool use at the savannah sites of Assirik in Senegal and Ugalla in
418 Tanzania did not fit the traditional predictions of the Necessity Hypothesis in that tool
419 use did not increase during periods of food scarcity (Hernandez-Aguilar, Moore et al. 2007,
420 Bogart and Pruetz 2011), but rather may be a necessary response to the lower overall
421 abundance of preferred resources in arid habitats.

422 Our comparison between Wamba and Goualougo revealed that availability of ripe
423 fruit, the main food of bonobos and chimpanzees, showed similar patterns of seasonal
424 fluctuation, and therefore did not support the Necessity Hypothesis to explain the *Pan*
425 difference in tool repertoires for feeding. The extent of fluctuation was somewhat greater
426 in Goualougo, suggesting that Goualougo chimpanzees might experience more severe
427 periods of fruit scarcity. However, Sanz and Morgan (Sanz and Morgan In press) reported
428 that frequency of tool use for feeding by chimpanzees in Goualougo was not related to the
429 proportion of fruiting trees, suggesting that this degree of difference in seasonal
430 fluctuation may not sufficiently explain the marked difference in tool use for feeding
431 between bonobos at Wamba and chimpanzees at Goualougo. During times of fruit scarcity,

both apes increased their consumption of terrestrial herbaceous vegetation and leaves which fit the profile of traditional fallback foods (Marshall and Wrangham 2007). Recent research also showed that there is no substantial difference in the kind and use of fallback food between chimpanzees and bonobos (Harrison and Marshall 2011). Furthermore, unpublished data by KK and DM showed that the density of terrestrial herbs was not higher in Wamba than in Goualougo (Wamba: 230 plots of 2x2m, 1.51± 2.10 stems of Marantaceae and Zingiberaceae/m^2; Goualougo: 7 plots of 5x50m, 2.08± 0.74 stems of herbs/m^2). Hence, it is unlikely that the availability of fallback foods during fruit scarcity explains the lack of tool use for feeding in bonobos.

According to the Opportunity Hypothesis, tool use is related to the frequency of encounters with particular tool targets (termites, ants, honey, etc.) or tool materials that may vary seasonally or between sites. For example, a higher abundance of arboreal insects provided increased opportunities for orangutans to invent tool use at Suaq Balimbing compared to other sites (Fox, van Schaik et al. 2004). Termite gathering by chimpanzees at Gombe is also thought to be opportunistic, as it occurs during the rainy season when termites are more accessible (McGrew, Tutin et al. 1979, McGrew and Collins 1985). In contrast, termite fishing has been documented throughout the year at several sites within central Africa (Sabater Pi 1974, McGrew, Tutin et al. 1979, Sabater-Pi 1979, Suzuki, Kuroda et al. 1995, Deblauwe 2009). Termite mounds

(Macrotermes) are rare and peripheral to the chimpanzee range at Seringbara in Guinea and no evidence of tool use in termite predation has been detected within this population (Koops, McGrew et al. 2013). However, chimpanzees at Seringbara use tools to harvest army ants, which are both abundant and widespread across the area (Koops, McGrew et al. 2013).

Our study revealed that habitat type, vegetation, and seasonal variation in climate at Wamba and Goualougo are fairly similar, and we did not identify any obvious differences between the sites that would preclude the possibility for bonobo tool use for feeding. At the bonobo study site Lui Kotal, assessment of opportunities for insectivory revealed that the same tool use opportunities were present and in some cases exceeded abundances reported from chimpanzee sites (McGrew, Marchant et al. 2007). A detailed study assessing the availability of army ants, termites, nut producing trees and potential tool materials at Wamba is currently underway. Furthermore, the range of habitat types of chimpanzees and bonobos overlap almost completely from savannah to rain forest. Due to such large within-species variation and between-species overlap, it is difficult for the Opportunity Hypothesis to explain presence of tool use for feeding in all studied chimpanzee populations and almost complete absence of it in wild bonobos.

The Relative Profitability Hypothesis suggests that tools will be used to harvest embedded food items when the energetic benefits outweigh the gains from conventional

feeding of more easily accessible food items (Rutz, Bluff et al. 2010, Rutz and St Clair 2012). There are several indications that the energetic benefits of tool use exceed those of conventional feeding in birds (Tebbich, Taborsky et al. 2002, Rutz, Bluff et al. 2010). Nut cracking by chimpanzees has also been shown to be an energetically profitable behaviour, which can yield several thousand calories per day (Gunther and Boesch 1993). Contradictory to this Relative Profitability Hypothesis, past research has shown that some forms of chimpanzee tool use may not necessarily be the most efficient means of calorie or protein intake. For example, a detailed review of ant-fishing behaviour among chimpanzees at Mahale revealed negligible nutritional gain from ant-fishing which was suggested to be a 'leisure' activity (Nishie 2011). As mentioned above, bonobo tool use occurred mostly in the social and self-directed contexts, and therefore we had no information to examine the profitability of tool use for feeding in bonobos. A more comprehensive evaluation of bonobo diet and nutritional intake may reveal whether or not conventional feeding is more profitable for this species than employing tool-assisted strategies.

With regard to the Invention Hypothesis, it is predicted that more frequent or complex tool use will occur in settings with enhanced opportunities for social transmission. This hypothesis would explain the absence of tool use in bonobos if bonobos gather in smaller parties or have weaker social relations within their groups compared to

chimpanzees. Our comparison indicated, however, that bonobo parties at Wamba were larger than chimpanzee parties at Goualougo. A recent comparison of many study sites of chimpanzees and bonobos indicated that differences in party size between the species are not statistically significant but that female bonobos attend party gatherings much more frequently relative to the very low attendance ratio of female chimpanzees (Furuichi 2009). This seems like a prime social setting for the spread of technological traditions in bonobos. Especially, since studies have reported a female bias in tool use among wild chimpanzees (McGrew 1979, Lonsdorf 2005) and captive bonobos (Boose, White et al. 2013), which has yet to be documented among wild bonobos. Importantly, it remains to be established whether increased gregariousness in bonobos also reflects an increase in close-range social learning opportunities. Moreover, we need to assess how levels of gregariousness and party composition, and thus social learning opportunities, vary across feeding and non-feeding contexts in both chimpanzees and bonobos. Priority of access to food resources exhibited by bonobo females (Furuichi 1997, Surbeck and Hohmann 2013) may reduce the need for food gathering with tools. Furthermore, we may want to question whether the party size is indeed an important factor for transmission of tool behaviours. Studies from several sites, including Gombe and Goualougo (Lonsdorf 2006, Sanz and Morgan 2013), suggested that party sizes while termite fishing were relatively small, and the majority of parties were mothers with dependent offspring. If the transmission of tool

508 behaviours mainly occurred between mother and offspring but not among adults, the
509 party size may have no influence on tool behaviours even if the transmission of
510 technological information is important for the existence of tool use.

511 Thus, as far as we know from the current information, differences in ecological or
512 social conditions may fail to explain differences in bonobo and chimpanzee technological
513 repertoires. It might be because these behaviours evolved in past ecological and social
514 conditions that differ from contemporary settings. A recent study reported that
515 present-day geographical features failed to explain the genetic structure of bonobos, and
516 that current genetic diversity was formed by paleoenvironmental circumstances during
517 the Pleistocene (Kawamoto, Takemoto et al. 2013). During the Pleistocene Epoch which
518 began 2.5 million years ago, forested areas in Africa were reduced to smaller refugia
519 during glacial periods (Mayr and Ohara 1986, Plana 2004). Such environmental changes
520 became more conspicuous after 1 million years ago, which coincides with the divergence
521 of the bonobo and chimpanzee lineages (Won and Hey 2005). The range of ancestral
522 chimpanzees experienced more extensive drying and fragmentation of forests during the
523 late Pleistocene than the habitat of ancestral bonobos on the left bank of the Congo River
524 where large forest refugia were maintained even during dry periods. Therefore,
525 tool-assisted feeding might have had greater adaptive value for the ancestors of modern
526 chimpanzees who were coping with greater variability in food resource availability, more

arid habitats, and potentially increased competition with other species than past bonobo populations. It is also possible that feeding technology evolved independently in the different chimpanzee subspecies as they repeatedly experienced dry periods. In their examination of tool use patterns among Ugandan chimpanzee populations, Gruber and colleagues (Gruber, Potts et al. 2012) suggested that ancestral chimpanzee populations in the region may have coped with harsher environments during the last Ice Age which may have prompted various behavioural innovations, such as extractive tool use. A major problem exists in this explanation however. If the ability for tool use evolved only in chimpanzees under certain conditions in the past, and therefore chimpanzees currently living in all types of habitats inherently use tools for feeding while bonobos in any type of habitat do not, then why is there no substantial difference in the ability for tool use under experimental conditions? This question needs to be further investigated through comparative studies both in the wild and captivity.

Although further studies are needed, it is possible that the differences in tool using propensities between chimpanzees and bonobos in the wild reflect divergent behavioural predispositions rather than differences in cognitive abilities. Comparative studies of the physical and cognitive abilities of great apes have failed to explain the paucity of tool use by bonobos. Within captive settings, bonobo tool use repertoires are as large and diverse as chimpanzees (Gruber, Clay et al. 2010). This is unlike gorillas, who

546 use tools for feeding but acquire the behaviour more slowly and perform it less frequently
547 than chimpanzees, suggesting a species difference in predisposition (Boysen, Kuhlmeier
548 et al. 1999, Lonsdorf, Ross et al. 2009). Even in experimental settings where individuals
549 had limited experience with tools, both chimpanzees and bonobos demonstrated
550 understanding of tool functional properties (Herrmann, Wobber et al. 2008).

551 The species differences in cognition and behavioural propensities between
552 chimpanzees and bonobos were aptly expressed in a range of cognitive problem solving
553 tasks. Bonobos surpassed chimpanzees in solving tasks related to the social world (i.e.
554 theory of mind, understanding of social causality), whereas chimpanzees showed more
555 skill in tasks related to the physical world (i.e. use of tools, understanding of physical
556 causality) (Herrmann, Hare et al. 2010). In a comparison of several captive groups, the
557 only major difference between chimpanzee and bonobo tool use was that bonobos of all
558 age and sex classes used tools in a play context (Gruber, Clay et al. 2010). The propensity
559 of adult bonobos to engage in play is thought to reflect their neotenous nature, as well as
560 environmental conditions that afford leisure time and a behavioural preference for
561 certain types of social interaction.

562 As mentioned above, some chimpanzee tool use does not seem to be the most
563 effective means of increasing energy intake, but may be performed when individuals have
564 leisure time (Nishie 2011). On the other hand, bonobos spend much of their leisure time

565 in play and play is common among adults (Enomoto 1990, Palagi 2006). Such differences
566 in behavioural preference may explain why bonobos are likely to perform like
567 chimpanzees in experimental conditions, but do not regularly perform tool use in natural
568 settings. This potential difference in behavioural predispositions toward tool use could be
569 further investigated by comparing levels of object manipulation and exploratory tendency
570 in chimpanzees and bonobos (Koops et al., in prep.).

571 It has been proposed that we are currently living in the "Anthropocene Epoch"
572 which is shaped by human influences on the environment. Although apes have persisted
573 through shifting climatic condition, there is no historical analogue for the rate and degree
574 of environmental change caused by anthropogenic disturbances. The long-term survival
575 of wild bonobos and chimpanzees is increasingly endangered by poaching, habitat
576 destruction and conversion, and infectious diseases. The Disturbance Hypothesis
577 suggests that ape cultures are fragile and that anthropogenic disturbances may affect the
578 social mechanisms which maintain these traditions (van Schaik 2001). Recognizing the
579 conservation value of animal cultures, scientists have suggested specific strategies for
580 conserving and managing animals that learn socially and share cultures (Whitehead,
581 Rendell et al. 2004, Laiolo and Jovani 2007, Whitehead 2010). Such measures must be
582 implemented immediately if we hope to continue advancing our understanding of
583 behavioural diversity of our closest living relatives.

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843 Figure Captions

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845 Figure 1. Comparison of ecological variables at Wamba and Goualougo. (a) Upper lines
846 show monthly mean of daily maximum temperature, and lower lines show monthly mean
847 of daily minimum temperature. (b) Monthly rainfall. * in Goualougo indicates no rainfall
848 in the month. (c) Seasonal fluctuation in availability of ripe fruit resources at Wamba
849 and Goualougo. Values for Wamba show the number of clusters of ripe fallen fruit per km
850 of transect. Values for Goualougo show proportion of food trees with ripe fruit on the
851 ground. (d) Monthly mean of daily party sizes for the E1 group of bonobos at Wamba
852 and chimpanzees at Goualougo. Party size included adults, adolescents, and juveniles,
853 but excluded infants.